

Nekton Use of Submerged Aquatic Vegetation, Marsh, and Shallow Unvegetated Bottom in the Atchafalaya River Delta, a Louisiana Tidal Freshwater Ecosystem

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ABSTRACT: We sampled nekton (fishes and decapod crustaceans) in submerged aquatic vegetation (SAV) (*Potamogeton nodosus*, *Najas guadalupensis*), in emergent marsh vegetation (*Sagittaria* spp. and *Scirpus americanus*), and over unvegetated bottom associated with three islands in the Atchafalaya River Delta, Louisiana. The purpose of our study was to quantify nekton densities in these major aquatic habitat types and to document the relative importance of these areas to numerically dominant aquatic organisms. We collected a total of 33 species of fishes and 7 species of crustaceans in 298 1-m² throw trap samples taken over three seasons: summer (July and August 1994), fall (September and October 1994), and spring (May and June 1995). Fishes numerically accounted for > 65% of the total organisms collected. Vegetated areas generally supported much higher nekton densities than unvegetated sites, although bay anchovies *Anchoa mitchilli* were more abundant over unvegetated bottom than in most vegetated habitat types. Among vegetation types, most species showed no apparent preference between SAV and marsh. However, inland silversides *Menidia beryllina* and freshwater gobies *Gobionellus shufeldti* were most abundant in *Scirpus* marsh in summer, and blue crabs *Callinectes sapidus* were most abundant in SAV (*Potamogeton*) in spring. Several species (sheepshead minnow *Cyprinodon variegatus*, rainwater killifish *Lucania parva*, and blue crab) apparently selected the vegetated backmarsh of islands (opposite of riverside) over streamside *Scirpus* marsh. Freshwater gobies, in contrast, were most abundant in streamside *Scirpus* marsh. Densities of juvenile blue crabs were high (up to 17 m⁻²) in vegetated delta habitat types and comparable to values reported from more saline regions of Gulf Coast estuaries. Shallow vegetated habitat types of the Atchafalaya River Delta and other tidal freshwater systems of the Gulf Coast may be important nursery areas for blue crabs and other estuarine species.

Introduction

Within the tidal freshwater region of estuaries, submerged aquatic vegetation (SAV) and emergent marsh are important habitats that provide nekton (fishes and decapod crustaceans) with food and refuge from predators (McIvor and Odum 1988; Rozas and Odum 1988; Yozzo and Odum 1993). Although the habitat value of tidal freshwater marsh and SAV in U.S. Atlantic coast estuaries is well documented, studies of tidal freshwater environments along the northern Gulf of Mexico have been restricted to sampling unvegetated bottom using trawls and seines (Juneau 1975; Hoese 1976; Thompson and Deegan 1983). Additional research is necessary in Gulf Coast estuaries to directly assess the value of vegetated tidal freshwater habitat.

Research that is most needed are interhabitat comparisons in which major habitat types within a tidal freshwater area are sampled concurrently using quantitative gear (Rozas and Minello 1997). Such studies would provide information on the relative quality of different vegetated tidal freshwater habitat types, which is generally unknown. Prior to initiating our study, interhabitat comparisons within tidal freshwater environments were limited to studies comparing nekton use between SAV and unvegetated bottom (Rozas and Odum 1987a) or between tidal creeks and the marsh surface (Rozas et al. 1988).

Information provided by interhabitat comparisons is essential for stewardship of living estuarine resources. For example, knowledge about the relative value of habitat types would be useful in designating essential fish habitat (Minello 1999) or for planning restoration projects in tidal freshwater areas. Restoration plans for projects with a goal of enhancing fishery production could emphasize

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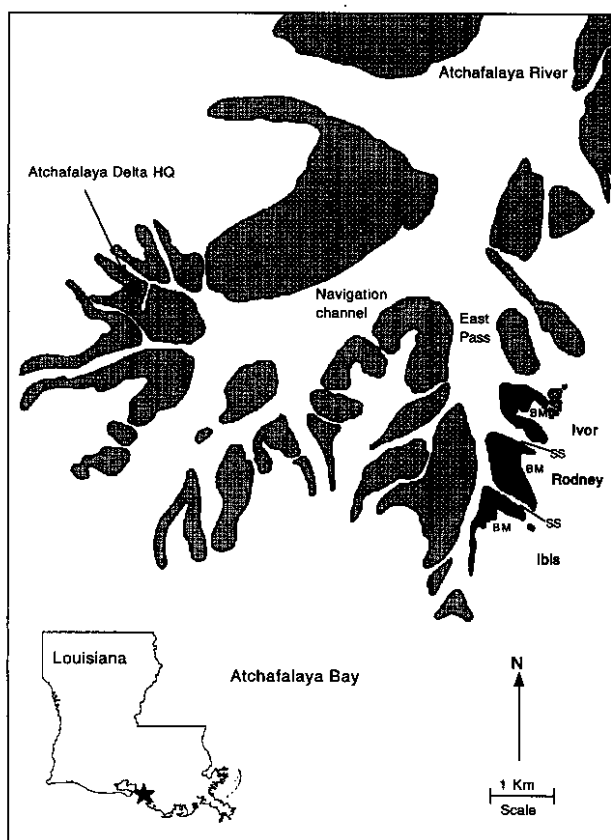


Fig. 1. Map of the study area showing its location along the Louisiana coast. We sampled six habitat types among the three islands shown in black. Backmarsh (BM) habitat types occur behind the islands, whereas the streamside (SS) habitat type is present along the south side of channels between Ivor Island and Rodney Island and between Rodney Island and Ibis Island. The Amerada Hess tide gauge is located near the Louisiana Department of Wildlife and Fisheries Atchafalaya Delta headquarters (HQ; 29°27'12.9"N, 91°20'39.6"W).

those habitat types that are most important for targeted species.

The objective of our study was to directly compare nekton use of shallow subtidal and low intertidal habitat types of a tidal freshwater system. We document the relative value of major tidal freshwater habitat types for nekton in the Atchafalaya River Delta by comparing nekton densities among SAV, flooded marsh, and unvegetated bottom. In addition, we describe the composition, relative abundance, and seasonal abundance of nekton associated with these habitat types.

Study Area

The study area is within the Atchafalaya River Delta located approximately 32 km south of Morgan City, Louisiana, near latitude 29°N and longitude 91°W (Fig. 1). Atchafalaya River flow controls salinities in the delta; during most of the year, sa-

linities in Atchafalaya Bay are below 0.5‰ (Orlando et al. 1993). Tides are predominantly diurnal and have a mean range of 0.2 m (U.S. Department of Commerce 1993); however, tidal effects may be overridden by meteorological factors or when river discharge is high. Typically, water temperatures in Atchafalaya Bay are below 15°C from December through early March and above 25°C from May through September. Atchafalaya Bay water is cooler than the waters of surrounding bays during normal river flows and up to 10°C cooler during high river discharge (Hoesle 1976).

We selected sample sites on three natural islands (Ivor, Rodney, and Ibis) located on the east side of East Pass (Fig. 1). The diverse vegetation on and around these islands consisted of at least 10 species of SAV and at least 7 species of emergent macrophytes (Castellanos personal observation). SAV occurred in both the subtidal and lowest intertidal areas and was dominated by *Potamogeton nodosus* and *Najas guadalupensis*. Other species of SAV (e.g., *Vallisneria americana* and *Heteranthera dubia*) were much less abundant and occurred only in widely scattered patches. Emergent vegetation was dominated by *Scirpus americanus* and additionally in the fall, by *Sagittaria platyphylla* and *Sagittaria latifolia*. Sparse stands of *S. platyphylla* occurred in the low intertidal; this species was replaced by *S. latifolia* at slightly higher elevations. Dense, monospecific stands of *Scirpus* occupied the highest intertidal areas. All habitat types occurred in the backmarsh of each island, the side of the island opposite East Pass and therefore protected from direct river flow (Fig. 1). *Scirpus* also occurred on island streamside along secondary river channels. Marsh and SAV habitat types were present from May through October. However, the areal coverage of habitat types varied seasonally from spring through fall. During winter months, the vegetation disappears because of either seasonal dieback or consumption by waterfowl (Fuller et al. 1985).

Materials and Methods

Each month, we selected the most abundant (according to visual survey) habitat types in the study area to sample. Over the course of our study, we sampled 6 major shallow water types including 2 dominated by SAV (*Potamogeton* and *Najas*), 3 dominated by emergent vegetation (*Sagittaria* spp., backmarsh *Scirpus*, and streamside *Scirpus*), and unvegetated bottom. *Sagittaria* marsh consisted of mixed stands of *S. platyphylla* and *S. latifolia*; these species were treated as one habitat type because herbivory by nutria *Myocastor coypus* rendered them morphologically similar and made distinguishing between the species difficult.

We sampled nekton (fishes and decapod crus-

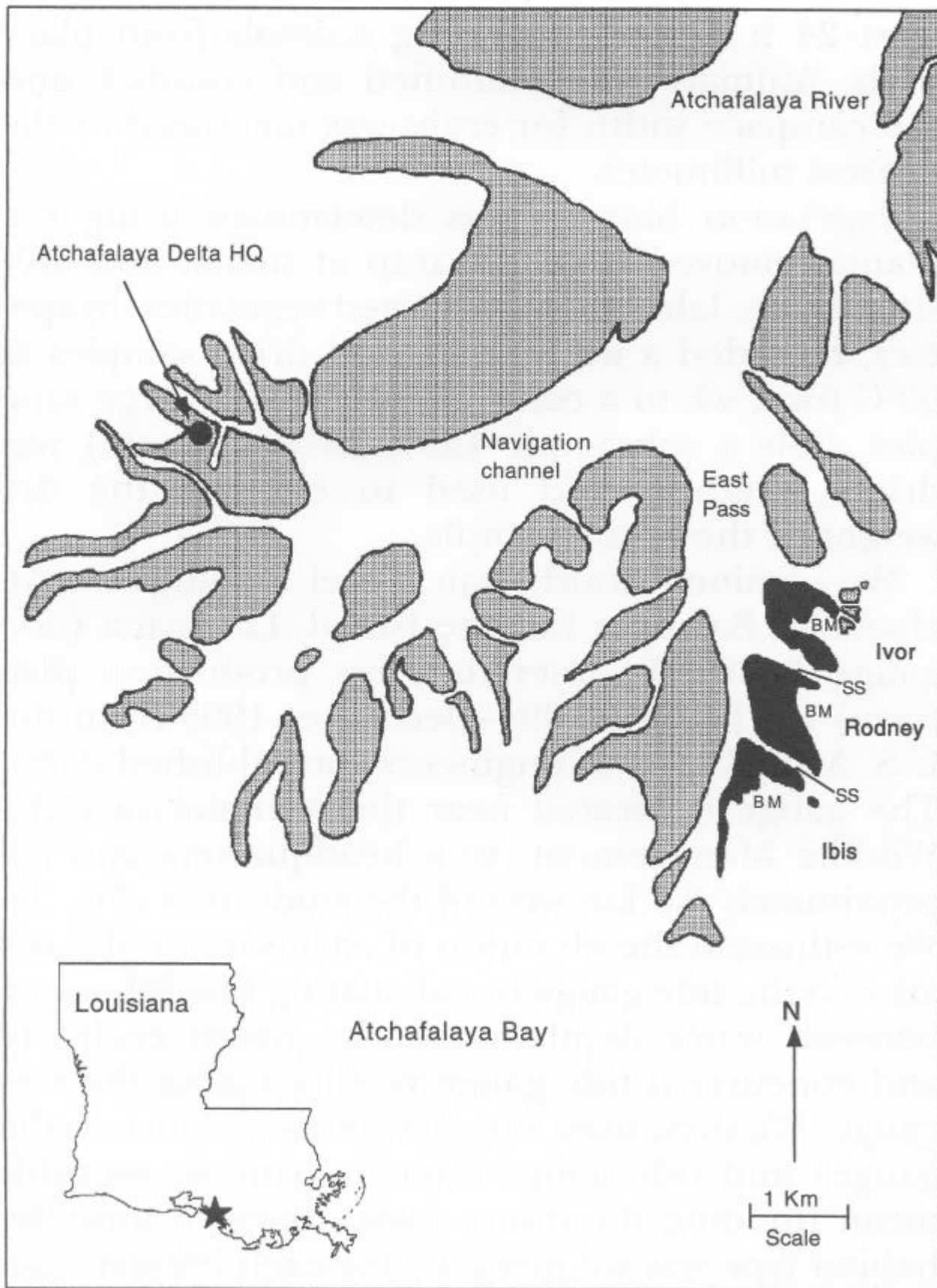


Figure 1.

taceans) using a 1-m² solid wall, aluminum throw trap at high tide when all habitat types were flooded and therefore available to aquatic organisms (Kushlan 1981; Rozas and Odum 1987a). The throw trap provides a standard quantitative sample in shallow water, performs similarly in vegetated and unvegetated habitats, and does not have the bias of permanent samplers caused by added structure in unvegetated habitats (Jordan et al. 1997; Rozas and Minello 1997).

On the basis of a preliminary study for estimating sample size (Castellanos 1997), we collected 12 samples each month (July–October 1994 and May–June 1995) from each dominant habitat type at randomly selected sites among three islands (Ivor, Rodney, and Ibis). We based the number of samples collected at each island in a particular habitat type on the ratio of the area of a habitat type at an island to the total area of the habitat type (all three islands combined) (Castellanos 1997). We sampled *Potamogeton* and backmarsh *Scirpus* every month during the sampling period (total of 6 mo), streamside *Scirpus* and unvegetated bottom 4 mo, *Najas* 3 mo, and *Sagittaria* 2 mo. Most habitat types occurred at all three islands in the study area; therefore, each month, we took samples of these habitat types at all three islands. However, we sampled backmarsh and streamside *Scirpus* only at Rodney Island and Ibis Island as *Scirpus* marsh was confined to these two islands. *Scirpus* samples were limited to approximately the first 2 m of the marsh edge.

Sample sites were slowly approached in a small, unpowered, aluminum boat. When approximately 3 m from the sample site, the trap was thrown from the bow of the boat. The trap was pushed into the sediment and checked for complete contact with the substrate. Prior to removal of animals trapped inside the sampler, we measured salinity (‰) and water temperature (°C) inside the trap with a Rosemount RS5-3 portable salinometer. We measured water depth inside the sampler to the nearest 0.5 cm with a meter stick. Vegetation enclosed in each sample was clipped at the sediment surface, removed, and stored on ice. We collected animals by sweeping the inside of the trap 10 times with a bar seine (1 × 1 m frame with 3-mm mesh nylon netting) that fit exactly inside the enclosure walls. Using sheepshead minnow *Cyprinodon variegatus* and Ohio river shrimp *Macrobrachium ohione* in efficiency experiments, we found that 10 sweeps were sufficient to remove most animals within the trap from SAV (both species = 100%) or emergent vegetation (fish = 99%, shrimp = 98%; Castellanos 1997).

Nekton samples were preserved in 10% formalin. In the laboratory, samples were rinsed for at

least 24 h before separating animals from plant parts. Animals were identified and counted, and the carapace width for crabs was measured to the nearest millimeter.

Vegetation biomass was determined using the plants removed from the trap at marsh and SAV sites. In the laboratory, we sorted vegetation by species, recorded a wet weight, and dried samples at 60°C for 2 wk to a constant weight. For large samples, only a subsample (25% of wet weight) was dried, weighed, and used to estimate the dry weight of the entire sample.

We obtained hourly water level readings for Atchafalaya Bay near Eugene Island, Louisiana (tide gauge # 88550, Amerada Hess production platform) for January 1994–December 1995 from the U.S. Army Corps of Engineers (unpublished data). The gauge is located near the Atchafalaya Delta Wildlife Management Area headquarters and approximately 5.8 km west of the study area (Fig. 1). We estimated the elevation of each sample site relative to the tide gauge by calculating the difference between water depth measurements at each site and concurrent tide gauge readings from the tide gauge. We then used site elevations (relative to the gauge) and tide gauge data to estimate monthly mean flooding durations (percentage of time the habitat type was submerged) for each habitat type. It should be noted that water depth is a cyclical condition of a habitat type in this tidal system. Mean water depths within a habitat type may be inconsistent, because it was not possible to measure this variable at all sample sites simultaneously despite our attempts to equally intersperse sampling across habitat types and time. Substrate elevation, estimated from the difference between tide gauge readings and concurrent water depths, is a more permanent characteristic and can be confidently compared among habitat types.

STATISTICAL ANALYSES

We considered consecutive months in which we sampled the same habitat types as a single sampling period or season (July and August = summer, September and October = fall, and May and June = spring). Data for each season were analyzed separately because the habitat types we sampled were only consistent within a season, and because some important nekton species were only abundant enough for statistical analysis in one season. All statistical analyses were performed using SAS (SAS Institute 1989). We used a multivariate analysis of variance (MANOVA) to test the null hypothesis that mean densities of numerically dominant species examined simultaneously were equal among habitat types. We conducted separate, univariate analysis of variance (3-way ANOVA; GLM

procedure) tests following significant MANOVA results (protected ANOVA; Scheiner 1993) to test the null hypothesis for individual species. We used the same statistical tests (protected ANOVA) to test the null hypothesis that means of environmental variables (salinity, water temperature, water depth, elevation) and vegetation biomass were equal among all habitat types. We also used ANOVA to test the null hypotheses that mean densities of total fishes and total crustaceans and mean sizes of blue crabs were equal among habitat types. In the ANOVA model, habitat type was the main effect (with 4 or 5 levels); the blocking factors, month and island, had two and three levels, respectively. Following a significant ANOVA analysis, the least square means (LSM) of habitat types were compared using the LSMEANS and PDIFF procedures because the data were not completely balanced (SAS Institute 1989). Density data were transformed using the Box-Cox procedure and blue crab size data were $\log(x + 1)$ transformed to improve normality and make the variances homogeneous prior to analysis. An alpha level of 0.05 was used for the MANOVA and ANOVA, but alpha was adjusted by the Bonferroni method (0.05 divided by the number of comparisons; Sokal and Rohlf 1995) for LSM comparisons to reduce the error introduced by making multiple comparisons. Tabular data presented in this paper are untransformed means. Data used to construct the figures were backtransformed to bring means used in the statistical analyses back to scale with the raw data (Sokal and Rohlf 1995).

Results

In 298 samples (94 in summer, 96 in fall, and 108 in spring), we collected a total of 26 species of fishes and 5 species of crustaceans in summer, 17 species of fishes and 7 species of crustaceans in fall, and 18 species of fishes and 4 species of crustaceans in spring (Table 1). Numerically, fishes represented > 65% of the total nekton collected, and most were taken in summer (2,121) and fall (2,008). Many fewer fishes were collected in the spring (218). The total catch of crustaceans was highest in the fall (1,491), largely due to an influx of juvenile blue crabs into the study area; crustaceans were less than half as numerous in either summer (539) or spring (249) than fall (Table 1). Mean densities of numerically dominant species (tested simultaneously) were significantly different among habitat types in summer (Wilks' Lambda = 0.26, $F_{21,233} = 6.74$; $p < 0.0001$), fall (Wilks' Lambda = 0.25, $F_{21,239} = 6.99$; $p < 0.0001$), and spring (Wilks' Lambda = 0.34, $F_{28,340} = 4.22$; $p < 0.0001$).

HABITAT USE: SUMMER

In summer 1994, *Najas* reached a peak in areal coverage and formed extensive beds over much of

the intertidal and shallow subtidal sections of the study area. *Potamogeton* also was prevalent at this time, but occurred as numerous isolated beds scattered throughout the study area. *Scirpus* was well established in both backmarsh and streamside areas.

Sheepshead minnows, rainwater killifish *Lucania parva*, inland silversides *Menidia beryllina*, and freshwater gobies *Gobionellus shufeldti* were numerically dominant in summer and accounted for 90% of the fishes collected at this time (Table 1). Mean densities of sheepshead minnows and rainwater killifish, which represented > 84% of the fishes collected in summer, were nearly evenly distributed among backmarsh habitat types and significantly greater in these habitat types than in streamside *Scirpus* (Fig. 2a and Table 1). Inland silversides and freshwater gobies were much less abundant overall (6% of total) and were most abundant in *Scirpus* marsh (Fig. 2a and Table 1); inland silversides were significantly more abundant in backmarsh *Scirpus* than all other habitat types, whereas freshwater gobies were significantly more abundant in streamside *Scirpus* than other habitat types (Fig. 2a).

Most (> 96% of total) crustaceans taken in summer were riverine grass shrimp *Palaemonetes paldosus*, blue crabs *Callinectes sapidus*, and Ohio river shrimp (Table 1). Blue crabs were most abundant in *Potamogeton* and backmarsh *Scirpus* (Fig. 2b). Riverine grass shrimp were significantly more abundant in *Potamogeton* than *Najas*, but densities in *Potamogeton* and other habitat types were not significantly different. Although we collected no Ohio river shrimp in *Najas*, mean densities of this species were not significantly different among habitat types (Fig. 2b).

HABITAT USE: FALL

In fall 1994, *Najas* began to disappear from the study area, leaving large areas of unvegetated mud bottom. *Potamogeton* was still present but in slightly smaller patches than in summer. *Sagittaria* occurred in backmarsh areas as dense, isolated patches (Ivor Island) or sparsely scattered over large areas (Rodney and Ibis Islands). Streamside *Scirpus* was still present, but inaccessible for sampling because wide, dense bands of water hyacinth *Eichhornia crassipes* was stranded at the edge of the marsh.

Sheepshead minnows, rainwater killifish, bay anchovies *Anchoa mitchilli*, and inland silversides were numerically dominant in fall and accounted for 92% of the fishes collected (Table 1). During fall, densities of sheepshead minnows and rainwater killifish were significantly greater in vegetated habitat types than over unvegetated bottom, but densities of these taxa were not significantly different among vegetated habitat types (Fig. 3a). In con-

TABLE 1. Untransformed mean (SE) density in numbers m^{-2} for fishes and crustaceans by habitat type and season. The total catch, total number of animals collected in all habitat types combined, and number of fish and crustacean species collected are also listed. Each mean was calculated from 24 samples except 22 samples for streamside *Scirpus* in summer 1994 and 12 for *Najas* in spring 1995. Relative abundance (RA) is given for those species with at least 1% relative abundance. Results (p values) of MANOVA Wilks' Lambda and ANOVA tests (considered significant at $p < 0.05$) comparing mean densities among habitat types within a season are given for each taxa included in the analyses. Blank spaces represent seasons in which habitat types were not dominant and therefore not sampled.

Species	Potamogeton nodosus	Najas guadalupensis	Backmarsh Scirpus americanus	Streamside Scirpus americanus	Sagittaria	Unvegetated	Total Catch	RA (%)	ANOVA
Summer 1994 (MANOVA $p < 0.0001$)									
Fishes (Total spp. = 26)									
Number of species	3.1 (0.24)	2.9 (0.16)	3.4 (0.31)	2.3 (0.33)					
<i>Cyprinodon variegatus</i>	11.5 (2.98)	17.6 (6.77)	15.0 (3.75)	0.5 (0.31)			1,070	50.4	0.0001
<i>Lucania parva</i>	10.0 (1.72)	10.8 (2.42)	7.8 (2.47)	1.3 (0.49)			716	33.8	0.0001
<i>Menidia beryllina</i>	0.4 (0.20)	0.0 (0.04)	2.2 (0.77)	0.1 (0.09)			65	3.1	0.0001
<i>Gobionellus shufeldti</i>	0.4 (0.21)	0.2 (0.10)	0.7 (0.51)	1.5 (0.72)			64	3.0	0.0015
<i>Fundulus grandis</i>	0.5 (0.21)	0.0 (0.04)	1.2 (0.31)	0.8 (0.35)			61	2.9	
<i>Gambusia affinis</i>	0.2 (0.43)	0.6 (0.42)	0.3 (0.17)	0.7 (0.46)			41	1.9	
<i>Myrophis punctatus</i>	0.5 (0.16)	0.4 (0.12)	0.1 (0.07)	0.2 (0.13)			29	1.4	
<i>Heterandria formosa</i>	0.1 (0.06)	0.0 (0.04)	0.3 (0.21)	0.6 (0.35)			23	1.1	
<i>Anchoa mitchilli</i>	0.0	0.2 (0.13)	0.2 (0.17)	0.1 (0.05)			9		
<i>Mugil cephalus</i>	0.0	0.3 (0.33)	0.0	0.0			8		
<i>Dormitator maculatus</i>	0.0	0.1 (0.08)	0.0 (0.04)	0.1 (0.08)			6		
<i>Dorosoma cepedianum</i>	0.0	0.1 (0.07)	0.1 (0.08)	0.0			5		
<i>Fundulus</i> sp.	0.0 (0.04)	0.1 (0.08)	0.1 (0.08)	0.0			5		
<i>Lepomis macrochirus</i>	0.1 (0.13)	0.0	0.0	0.0			3		
<i>Micropterus punctulatus</i>	0.1 (0.08)	0.0	0.0	0.0			2		
<i>Lepisosteus oculatus</i>	0.1 (0.06)	0.0	0.0	0.0			2		
Gobiidae sp.	0.0	0.0	0.0 (0.04)	0.0 (0.05)			2		
<i>Gobionellus boleosoma</i>	0.1 (0.06)	0.0	0.0	0.0			2		
<i>Gobionellus oceanicus</i>	0.0	0.0	0.0 (0.04)	0.0			1		
<i>Evorthodus lyricus</i>	0.0	0.0	0.0	0.0 (0.05)			1		
<i>Membras martinica</i>	0.0	0.0 (0.04)	0.0	0.0			1		
<i>Elops saurus</i>	0.0	0.0 (0.04)	0.0	0.0			1		
<i>Elassoma zonatum</i>	0.0	0.0	0.0 (0.04)	0.0			1		
<i>Trinectes maculatus</i>	0.0	0.0	0.0	0.0 (0.05)			1		
<i>Fundulus chrysotus</i>	0.0	0.0	0.0	0.0 (0.05)			1		
Sciaenidae sp.	0.0	0.0	0.0	0.0 (0.05)			1		
TOTAL FISHES	24.0 (3.40)	30.5 (7.49)	28.2 (4.94)	6.2 (0.98)			2,121		0.0001
Crustaceans (Total spp. = 5)									
Number of species	1.6 (0.17)	0.6 (0.12)	1.0 (0.17)	1.0 (0.23)					
<i>Palaemonetes pabulosus</i>	7.6 (3.44)	0.8 (0.49)	0.3 (0.15)	1.2 (0.70)			233	43.2	0.0081
<i>Callinectes sapidus</i>	4.9 (1.23)	1.0 (0.37)	3.3 (0.96)	0.4 (0.16)			228	42.3	0.0001
<i>Macrobrachium ohione</i>	0.5 (0.27)	0.0	1.8 (1.75)	0.2 (0.11)			61	11.3	0.1307
Crayfish spp.	0.2 (0.13)	0.2 (0.17)	0.0 (0.04)	0.0 (0.05)			11	2.0	
<i>Uca</i> spp.	0.0	0.0	0.0	0.3 (0.15)			6	1.1	
TOTAL CRUSTACEANS	13.2 (3.62)	2.0 (0.57)	5.4 (1.96)	2.1 (0.78)			539		0.0002
Fall 1994 (MANOVA $p < 0.0001$)									
Fishes (Total spp. = 17)									
Number of species	3.3 (0.21)		3.1 (0.28)		3.3 (0.22)	1.5 (0.22)			
<i>Cyprinodon variegatus</i>	10.0 (2.43)		22.7 (4.87)		15.5 (5.72)	0.3 (0.16)	1,164	58.0	0.0001
<i>Lucania parva</i>	6.7 (1.49)		3.6 (1.30)		8.1 (2.69)	0.1 (0.09)	445	22.2	0.0001
<i>Anchoa mitchilli</i>	1.8 (1.06)		0.7 (0.33)		0.7 (0.44)	1.8 (0.70)	120	6.0	0.0096
<i>Menidia beryllina</i>	0.6 (0.27)		1.8 (0.61)		2.0 (0.75)	0.5 (0.26)	116	5.8	0.0277
<i>Gobionellus boleosoma</i>	1.0 (0.29)		0.1 (0.09)		0.7 (0.29)	0.2 (0.10)	49	2.4	
<i>Gambusia affinis</i>	0.1 (0.07)		0.8 (0.75)		0.1 (0.07)	0.0	26	1.3	
<i>Gobionellus</i> sp.	0.8 (0.83)		0.0		0.0	0.0	20	1.0	
<i>Gobionellus oceanicus</i>	0.1 (0.07)		0.0		0.2 (0.10)	0.3 (0.14)	13		
<i>Fundulus grandis</i>	0.1 (0.08)		0.2 (0.10)		0.2 (0.17)	0.0	11		
<i>Myrophis punctatus</i>	0.2 (0.10)		0.1 (0.06)		0.1 (0.06)	0.0 (0.04)	10		
<i>Gobionellus shufeldti</i>	0.1 (0.06)		0.2 (0.13)		0.1 (0.06)	0.0	9		
<i>Heterandria formosa</i>	0.0		0.1 (0.08)		0.2 (0.15)	0.0	7		
<i>Mugil cephalus</i>	0.0		0.1 (0.09)		0.0 (0.04)	0.1 (0.09)	7		
<i>Fundulus</i> sp.	0.0		0.0 (0.04)		0.3 (0.14)	0.0	7		
Gerreidae sp.	0.0		0.0		0.0 (0.04)	0.0 (0.04)	2		
<i>Strongylura marina</i>	0.0		0.0 (0.04)		0.0	0.0	1		
<i>Dormitator maculatus</i>	0.0		0.0 (0.04)		0.0	0.0	1		
TOTAL FISHES	21.5 (3.18)		30.5 (5.56)		28.3 (6.04)	3.4 (0.81)	2,008		0.0001

TABLE 1. Continued.

Species	<i>Potamogeton nodosus</i>	<i>Najas guadalupensis</i>	Backmarsh <i>Scirpus americanus</i>	Streamside <i>Scirpus americanus</i>	<i>Sagittaria</i>	Unvegetated	Total Catch	RA (%)	ANOVA
Crustaceans (Total spp. = 7)									
Number of species	2.0 (0.17)		2.0 (0.26)		2.0 (0.22)	1.7 (0.12)			
<i>Callinectes sapidus</i>	16.9 (3.19)		11.5 (3.20)		13.5 (1.89)	1.4 (0.40)	1,039	69.7	0.0001
<i>Palaemonetes paludosus</i>	4.2 (1.81)		0.9 (0.39)		3.5 (1.64)	0.1 (0.13)	210	14.1	0.0016
<i>Macrobrachium ohione</i>	2.1 (0.66)		1.7 (1.07)		4.8 (2.68)	0.1 (0.08)	209	14.0	0.0044
Crayfish spp.	0.0		0.3 (0.19)		0.7 (0.33)	0.0	24	1.6	
<i>Uca</i> sp.	0.0		0.2 (0.17)		0.0	0.0	5		
Crab sp.	0.0		0.1 (0.07)		0.0	0.0	3		
Shrimp sp.	0.0		0.0 (0.04)		0.0	0.0	1		
TOTAL CRUSTACEANS	23.2 (3.8)		14.9 (3.83)		22.5 (4.70)	1.6 (0.44)	1,491		0.0001
Spring 1995 (MANOVA $p < 0.0001$)									
Fishes (Total spp. = 18)									
Number of species	1.8 (0.21)	1.7 (0.38)	1.0 (0.17)	1.2 (0.23)		0.8 (0.17)			
<i>Anchoa mitchilli</i>	0.7 (0.44)	1.2 (0.58)	0.5 (0.23)	0.8 (0.53)		0.6 (0.25)	75	34.4	0.8244
<i>Gobionellus shufeldti</i>	0.3 (0.13)	0.3 (0.13)	0.3 (0.13)	0.8 (0.20)		0.1 (0.07)	38	17.4	0.0758
<i>Myrophis punctatus</i>	0.7 (0.17)	0.4 (0.15)	0.1 (0.09)	0.2 (0.08)		0.1 (0.07)	31	14.2	0.0065
<i>Gobionellus boleosoma</i>	0.2 (0.10)	0.7 (0.26)	0.2 (0.10)	0.1 (0.09)		0.1 (0.06)	21	9.6	0.0302
<i>Mugil cephalus</i>	0.2 (0.08)	0.1 (0.08)	0.0 (0.00)	0.3 (0.22)		0.0 (0.04)	13	6.0	
<i>Menidia beryllina</i>	0.2 (0.10)	0.0	0.2 (0.10)	0.0 (0.04)		0.0 (0.04)	11	5.0	
<i>Citharichthys spilopterus</i>	0.0 (0.04)	0.0	0.1 (0.06)	0.2 (0.08)		0.1 (0.06)	9	4.1	
<i>Cyprinodon variegatus</i>	0.1 (0.06)	0.0	0.1 (0.08)	0.0 (0.04)		0.0	5	2.3	
<i>Lucania parva</i>	0.0	0.2 (0.11)	0.0 (0.04)	0.0		0.0	3	1.4	
<i>Gobionellus</i> sp.	0.0 (0.04)	0.0	0.0	0.0 (0.04)		0.0	2		
<i>Evorthodus byrcus</i>	0.1 (0.06)	0.0	0.0	0.0		0.0	2		
<i>Paralichthys lethostigma</i>	0.1 (0.06)	0.0	0.0	0.0		0.0	2		
<i>Leiostomus xanthurus</i>	0.0 (0.04)	0.0	0.0	0.0		0.0	1		
<i>Microgogonias undulatus</i>	0.0	0.0	0.0	0.0		0.0 (0.04)	1		
<i>Syngnathus</i> sp.	0.0 (0.04)	0.0	0.0	0.0		0.0	1		
<i>Elassoma zonatum</i>	0.0	0.0	0.0 (0.04)	0.0		0.0	1		
<i>Dorosoma cepedianum</i>	0.0	0.0	0.0	0.0		0.0 (0.04)	1		
<i>Heterandria formosa</i>	0.0	0.0	0.0 (0.04)	0.0		0.0	1		
TOTAL FISHES	2.6 (0.44)	2.8 (0.73)	1.5 (0.30)	2.4 (0.68)		1.2 (0.31)	218		0.0163
Crustaceans (Total spp. = 4)									
Number of species	1.8 (0.18)	0.9 (0.23)	0.5 (0.13)	0.6 (0.17)		0.2 (0.09)			
<i>Macrobrachium ohione</i>	3.2 (2.14)	1.0 (0.52)	0.1 (0.06)	1.7 (1.11)		0.0	310	52.2	0.0001
<i>Callinectes sapidus</i>	2.4 (0.34)	0.6 (0.26)	0.5 (0.18)	0.4 (0.16)		0.2 (0.09)	92	36.9	0.0001
<i>Palaemonetes paludosus</i>	0.6 (0.19)	0.1 (0.08)	0.0 (0.04)	0.4 (0.22)		0.0	26	10.4	0.0009
Crawfish sp.	0.0	0.0	0.0 (0.04)	0.0		0.0	1		
TOTAL CRUSTACEANS	6.2 (2.26)	1.7 (0.63)	0.7 (0.21)	2.5 (1.36)		0.2 (0.09)	249		0.0001

trast, bay anchovies were significantly more abundant over unvegetated bottom than in backmarsh *Scirpus* or *Sagittaria*, and densities over unvegetated bottom and in *Potamogeton* were not significantly different (Fig. 3a). Although the ANOVA was significant, densities of inland silversides were not detectably different among habitat types (Fig. 3a).

Blue crabs, riverine grass shrimp, and Ohio river shrimp were the numerically dominant species in fall as in summer, accounting for > 97% of total crustaceans collected (Table 1). Mean densities of blue crabs and riverine grass shrimp were significantly greater in all vegetated habitat types (and densities of Ohio river shrimp were significantly greater in *Potamogeton*) than over unvegetated bottom; however, densities of these taxa were not significantly different among vegetated habitat types (Fig. 3b).

HABITAT USE: SPRING

By spring 1995, SAV and emergent vegetation had begun to recover from the previous winter die-off and grazing by waterfowl. Large, dense patches of *Potamogeton* were established in the backmarsh and new stems of *Scirpus* occupied backmarsh and streamside areas of the study area. Patches of *Najas*, interspersed with an equal amount of unvegetated bottom, covered the intertidal and shallow subtidal areas of the study area where *Potamogeton* was absent.

During spring, numerically dominant fishes were bay anchovies, freshwater gobies, speckled worm eels *Myrophis punctatus*, and darter gobies *Gobionellus boleosoma*; together, these species accounted for > 75% of the total fishes (Table 1). Densities of speckled worm eels in *Potamogeton* (and den-

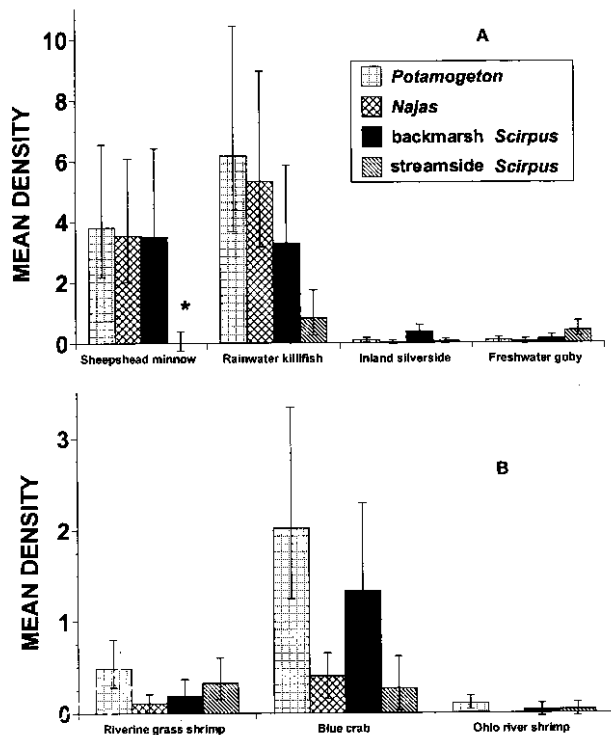


Fig. 2. A) Mean density (individuals m⁻²) of sheephead minnow *Cyprinodon variegatus*, rainwater killifish *Lucania parva*, inland silverside *Menidia beryllina*, and freshwater goby *Gobionellus shufeldti* collected in summer 1994 from *Potamogeton*, *Najas*, backmarsh *Scirpus*, and streamside *Scirpus* habitat types. An asterisk indicates a least square mean that was negative and was set to zero for clarity. B) Mean density (individuals m⁻²) of riverine grass shrimp *Palaemonetes padosus*, blue crab *Callinectes sapidus*, and Ohio river shrimp *Macrobrachium ohioense* collected in summer 1994 from *Potamogeton*, *Najas*, backmarsh *Scirpus*, and streamside *Scirpus* habitat types. Least square means and confidence limits of transformed data for both A and B were calculated from 22 samples of streamside *Scirpus* and 24 samples of all other habitat types. Back-transformed means and confidence limits are presented. Error bars = 95% confidence interval.

sities of darter gobies in *Najas*) were significantly greater than densities of these species over unvegetated bottom (Fig. 4a). Speckled worm eels were significantly more abundant in *Potamogeton* than backmarsh *Scirpus*, but densities among *Potamogeton* and other vegetated habitat types were not significantly different. Densities of darter gobies were significantly greater in *Najas* than streamside *Scirpus*, but differences in densities among *Najas* and other vegetated habitat types were not detected. Mean densities of bay anchovies and freshwater gobies were not significantly different among habitat types (Fig. 4a).

As in summer and fall, Ohio river shrimp, blue crabs, and riverine grass shrimp numerically dominated crustacean assemblages in spring, accounting for > 99% of the total catch (Table 1). Blue crab densities were significantly greater in *Potamo-*

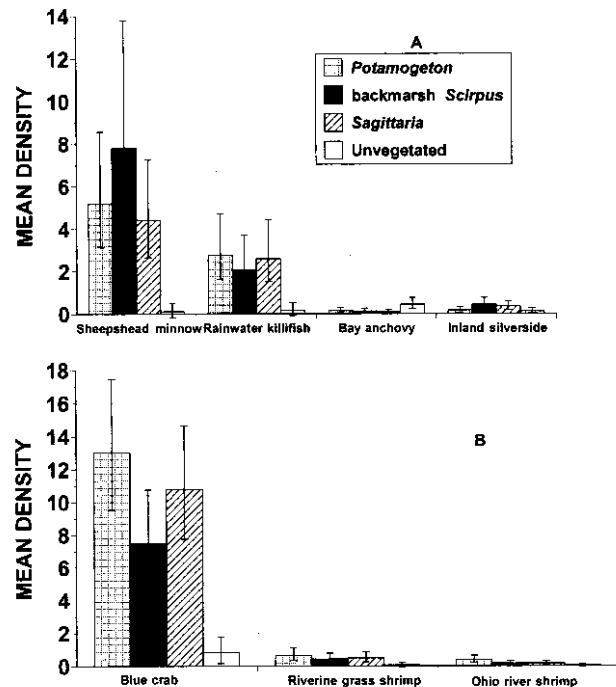


Fig. 3. A) Mean density (individuals m⁻²) of sheephead minnow *Cyprinodon variegatus*, rainwater killifish *Lucania parva*, bay anchovy *Anchoa mitchilli*, and inland silverside *Menidia beryllina* collected in fall 1994 from *Potamogeton*, backmarsh *Scirpus*, *Sagittaria*, and unvegetated bottom. B) Mean density (individuals m⁻²) of blue crab *Callinectes sapidus*, riverine grass shrimp *Palaemonetes padosus*, and Ohio river shrimp *Macrobrachium ohioense* collected in fall 1994 from *Potamogeton*, backmarsh *Scirpus*, *Sagittaria*, and unvegetated bottom. Least square means and confidence limits of transformed data for both A and B were calculated from 24 samples. Back-transformed means and confidence limits are presented. Error bars = 95% confidence interval.

geton than all other habitat types (Fig. 4b). Riverine grass shrimp were significantly more abundant in *Potamogeton* than *Najas*, and Ohio river shrimp were significantly more abundant in *Potamogeton* than backmarsh *Scirpus*, however, densities of these two species among *Potamogeton* and other vegetated habitat types were not significantly different (Fig. 4b). All three numerically dominant crustacean species were significantly more abundant in *Potamogeton* than over unvegetated bottom, and we collected no riverine grass shrimp or Ohio river shrimp at unvegetated sites (Fig. 4b).

BLUE CRAB SIZE

Blue crab mean size (carapace width) was significantly different among habitat types in summer and spring. In summer, blue crab mean size was significantly greater in streamside *Scirpus* than in all other habitat types, but mean sizes among habitat types other than streamside *Scirpus* were not significantly different (Table 2). Mean sizes of blue

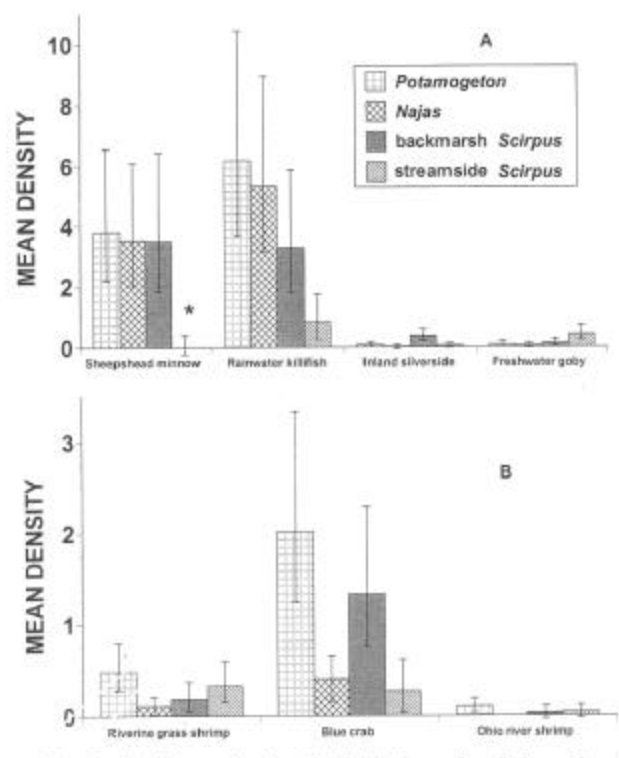


Figure 2.

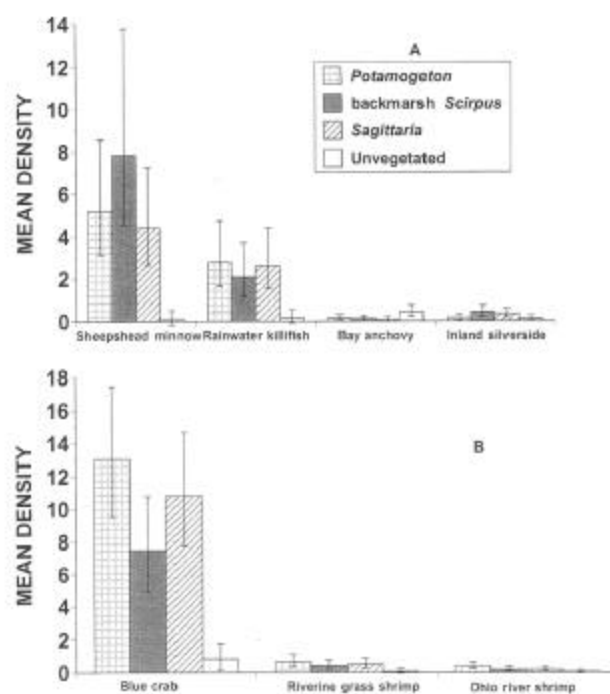
Fig. 3. A) Mean density (individuals m⁻²) of sheephead minnow *Cyprinodon variegatus*, rainwater killifish *Turania horni*.

Figure 3.

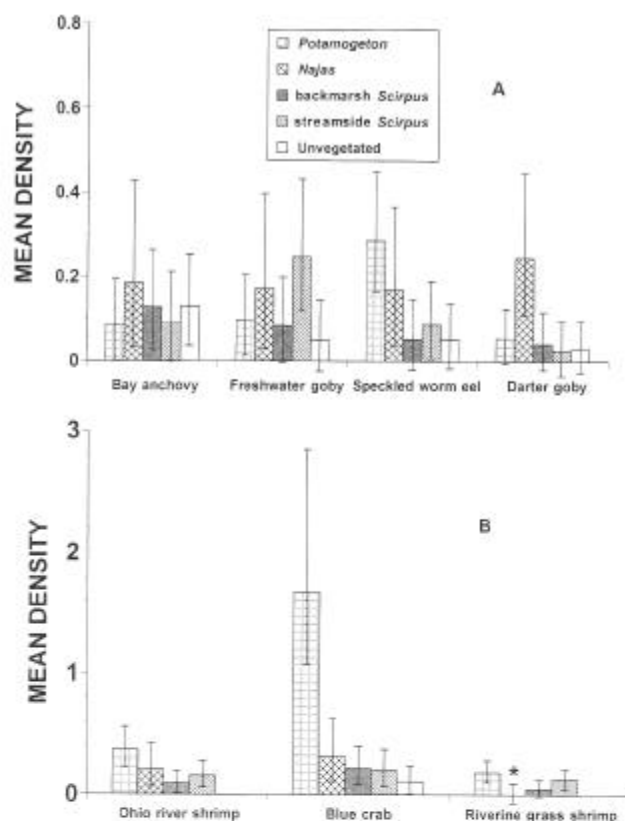


Fig. 4. A) Mean density (individuals m^{-2}) of bay anchovy *Anchoa mitchilli*, freshwater goby *Gobionellus shufeldti*, speckled worm eel *Myrophis punctatus*, and darter goby *Gobionellus boleosoma* collected in spring 1995 from *Potamogeton*, *Najas*, backmarsh *Scirpus*, streamside *Scirpus*, and unvegetated bottom. B) Mean density (individuals m^{-2}) of Ohio river shrimp *Macrobrachium ohione*, blue crab *Callinectes sapidus*, and riverine grass shrimp *Palaemonetes paludosus* collected in spring 1995 from *Potamogeton*, *Najas*, backmarsh *Scirpus*, streamside *Scirpus*, and unvegetated habitats. Least square means and confidence limits of transformed data for both A and B were calculated from 12 samples of *Najas* and 24 samples of all other habitat types. Back-transformed means and confidence limits are presented. Error bars = 95% confidence interval. An asterisk indicates a least square mean that was negative and was set to zero for clarity.

crabs were not significantly different among habitat types in the fall. In spring, blue crab mean sizes were significantly greater in streamside *Scirpus* than *Potamogeton* and unvegetated bottom, but mean siz-

es in streamside *Scirpus*, *Najas*, and backmarsh *Scirpus* were not significantly different.

ENVIRONMENTAL VARIABLES

Environmental conditions within the study area differed seasonally. Mean salinities and mean water depths were greatest in fall, whereas mean temperatures and mean vegetation biomasses were greatest in summer (Table 3).

Moreover, within a season, environmental variables differed among habitat types (Table 4). Mean variable values (tested simultaneously) were significantly different among habitat types in summer (Wilks' Lambda = 0.46, $F_{15,230} = 4.95$; $p < 0.0001$), fall (Wilks' Lambda = 0.16, $F_{15,235} = 14.64$; $p < 0.0001$), and spring (Wilks' Lambda = 0.05, $F_{20,919} = 22.31$; $p < 0.0001$). In both seasons (summer and spring) that streamside *Scirpus* was sampled, this habitat type had lower mean water temperatures than all other habitat types (except *Najas* in summer). Substrate elevations (and mean water depths) in SAV and unvegetated habitat types were not significantly different; however, unvegetated bottom was significantly lower in elevation and flooded more deeply than emergent marsh (fall and spring, Tables 3 and 4). Mean water depth was significantly greater in SAV (*Potamogeton* and *Najas*) than streamside *Scirpus*. Backmarsh *Scirpus* had significantly less standing biomass and lower stem density than streamside *Scirpus* (summer and spring), but more biomass than *Sagittaria* (fall). Mean vegetation biomass of *Potamogeton* was significantly greater than that of *Najas* in spring, but mean biomasses of the two SAV habitat types were not significantly different in summer (Table 4).

Flooding durations were higher in spring and fall than in summer, and the difference in mean flooding duration among habitat types was relatively consistent for months within a season (Fig. 5). Submerged aquatic vegetation and unvegetated bottom had the highest flooding durations; in spring and fall when both habitat types were sampled, SAV and unvegetated bottom were almost constantly flooded (> 94%). In summer, SAV was flooded > 75% of the time. Emergent vegetation

TABLE 2. Mean sizes, carapace width (mm), and SE, untransformed data, of blue crabs taken in each habitat type sampled during each season. Each mean for a habitat type was estimated from the mean size in n samples that contained blue crabs. The p value listed is from an ANOVA comparing mean size among habitat types that were sampled in a given season.

Season	<i>Potamogeton nodosus</i>			<i>Najas guadalupensis</i>			Backmarsh <i>Scirpus americanus</i>			Streamside <i>Scirpus americanus</i>			<i>Sagittaria</i>			Unvegetated			p
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	
Summer	16.8	(1.09)	19	17.4	(3.67)	10	18.1	(2.69)	16	30.0	(7.85)	7							0.0072
Fall	12.1	(0.74)	24				11.0	(0.54)	22				12.0	(0.68)	24	11.1	0.99	13	0.9927
Spring	17.1	(1.30)	23	22.5	(4.37)	5	19.9	(3.43)	7	26.9	(5.03)	7				12.8	(1.85)	5	0.0024

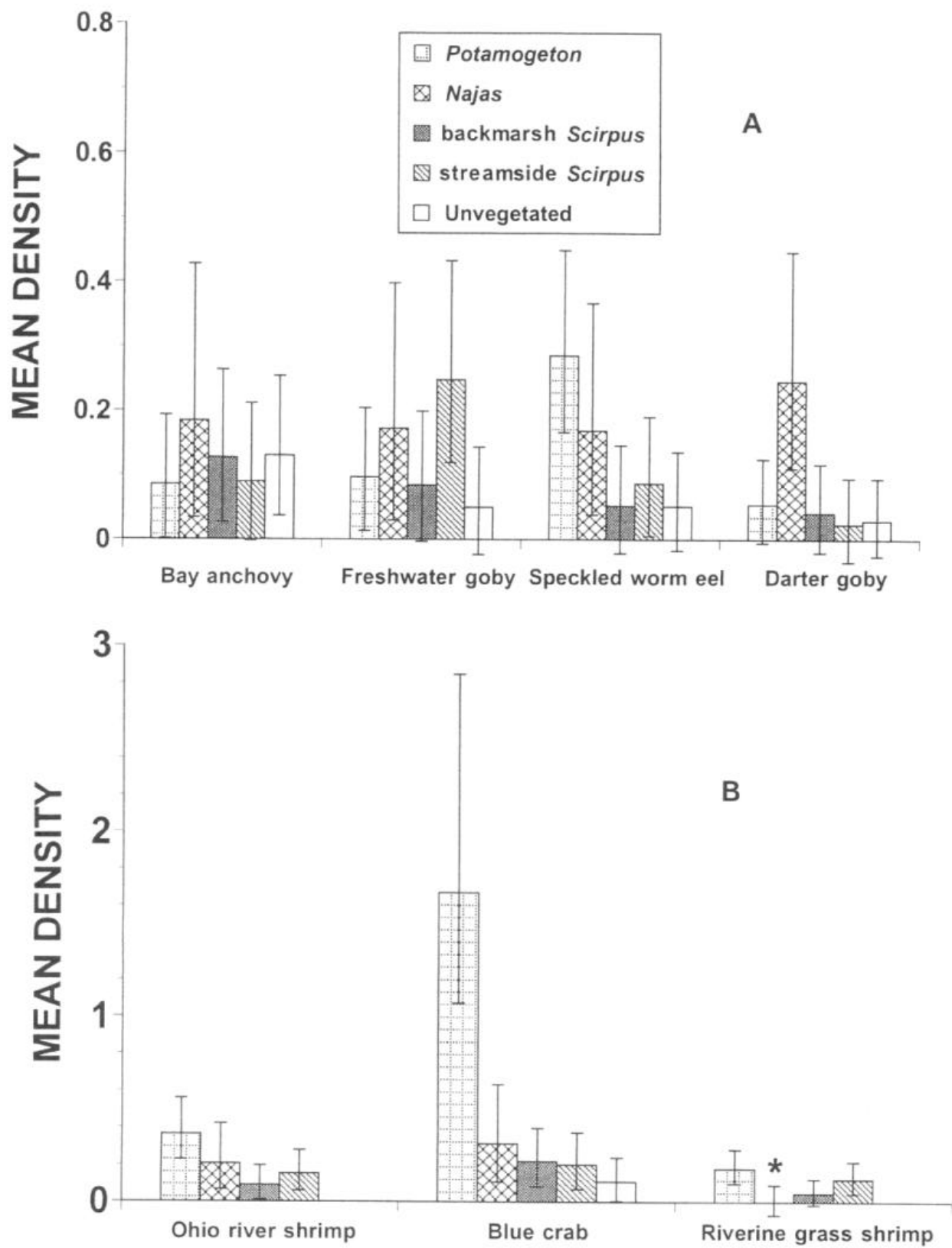


Figure 4.

TABLE 3. Means with SE, untransformed data, of environmental and vegetation (biomass and stem density for *Scirpus americanus* in summer and spring) variables for each habitat type and season. Each mean was calculated from 24 samples except 22 samples for streamside *S. americanus* and 12 for *Najas guadalupensis* in Spring 1995. Means for salinity in summer and spring were within the accuracy range of the salinometer and therefore, they were not included in the statistical analyses. Results (p values) of MANOVA Wilks' Lambda and ANOVA tests (considered significant at $p < 0.05$) comparing mean measurements among habitat types within a season are given for each variable. Blank spaces represent seasons in which habitats were not dominant and therefore not sampled.

Variable	<i>Potamogeton nodosus</i>	<i>Najas guadalupensis</i>	Backmarsh <i>Scirpus americanus</i>	Streamside <i>Scirpus americanus</i>	<i>Sagittaria</i>	Unvegetated	MANOVA	ANOVA
Summer 1994							0.0001	
Salinity (‰)	0.2 (0.01)	0.2 (0.01)	0.3 (0.01)	0.3 (0.01)				
Temperature (°C)	31.4 (0.42)	30.6 (0.64)	31.3 (0.44)	29.3 (0.28)				0.0030
Water depth (cm)	28.8 (1.76)	30.9 (1.98)	25.3 (1.29)	16.7 (0.96)				0.0001
Elevation (cm)	13.4 (1.89)	12.2 (1.87)	19.7 (1.05)	20.9 (1.60)				0.1242
Vegetation biomass (g m ⁻²)	40.6 (5.15)	36.4 (6.59)	43.0 (7.79)	104.2 (14.11)				0.0001
Stem density (# m ⁻²)			68.8 (8.77)	134.7 (28.72)				0.0077
Fall 1994							0.0001	
Salinity (‰)	1.3 (0.27)		1.7 (0.30)		1.0 (0.23)	1.4 (0.29)		0.1996
Temperature (°C)	27.9 (0.43)		27.4 (0.34)		26.8 (0.41)	27.3 (0.37)		0.0482
Water depth (cm)	41.0 (1.81)		37.8 (1.64)		35.9 (1.53)	43.6 (1.40)		0.0016
Elevation (cm)	2.9 (1.75)		9.6 (1.38)		6.1 (2.08)	1.6 (1.56)		0.0072
Vegetation biomass (g m ⁻²)	21.9 (2.61)		72.2 (18.62)		27.1 (4.82)			0.0019
Spring 1995							0.0001	
Salinity (‰)	0.2 (0.01)	0.2 (0.01)	0.2 (0.01)	0.2 (0.00)		0.2 (0.01)		
Temperature (°C)	28.5 (0.35)	28.5 (0.31)	29.1 (0.42)	25.5 (0.11)		28.5 (0.40)		0.0001
Water depth (cm)	31.5 (1.82)	30.3 (1.10)	20.4 (1.32)	17.6 (1.17)		31.1 (2.06)		0.0001
Elevation (cm)	13.6 (1.60)	21.9 (1.40)	25.8 (1.65)	33.2 (1.40)		14.7 (1.68)		0.0001
Vegetation biomass (g m ⁻²)	14.0 (1.18)	2.3 (0.43)	18.4 (3.88)	50.3 (10.36)				0.0001
Stem density (# m ⁻²)			89.5 (16.52)	184.37 (23.64)				0.0001

was flooded for shorter periods than SAV or unvegetated bottom, but flooding durations for all emergent habitat types (except streamside *Scirpus*) also were long (> 70%). Except for July, streamside *Scirpus* had the shortest flooding durations of all habitat types (61–77%).

Discussion

Although densities of most nektonic species in the Atchafalaya River Delta differed among shallow estuarine habitat types, a clear difference in habitat use between flooded marsh and SAV was not observed for most species. Only three species showed an apparent habitat preference between flooded marsh and SAV. Inland silversides and freshwater

gobies were most abundant in *Scirpus* marsh in summer, whereas blue crabs were most abundant in SAV (*Potamogeton*) in spring. Direct comparisons of nekton populations between SAV and flooded marsh are few. Two such studies were limited to blue crabs (Thomas et al. 1990; Heck et al. 1994), and only one examined entire assemblages of nekton (Rozas and Minello 1998). Thomas et al. (1990) found significantly greater densities of blue crabs in seagrass than salt marsh for 7 of 12 mo sampled, but Heck et al. (1994) did not find consistent differences in average monthly crab densities between SAV and salt marsh. In a study of a south Texas estuary, numerically dominant fish and decapod crustacean densities were either sig-

TABLE 4. Results of least square means comparison tests on significant ($p < 0.05$) ANOVA test results of environmental variables. Nonsignificant ANOVA tests are indicated by NS. Habitat types are listed in descending order of mean variable values. Means that did not differ significantly at $p < 0.0083$ ($p < 0.005$ for Spring) are joined by a line. Habitat types are represented as follows: PN = *Potamogeton nodosus*, NG = *Najas guadalupensis*, BSA = *Scirpus americanus* (backmarsh), SSA = *Scirpus americanus* (streamside), SG = *Sagittaria*, and UN = unvegetated.

Variable	Summer 1994	Fall 1994	Spring 1995
Salinity	NS	NS	NS
Water temperature	PN BSA NG SSA	PN BSA UN SG	NG BSA UN PN SSA
Water depth	NG PN BSA SSA	UN PN BSA SG	NG PN UN BSA SSA
Elevation	NS	BSA SG PN UN	SSA BSA NG UN PN
Vegetation biomass	SSA BSA PN NG	BSA SG PN	SSA BSA PN NG

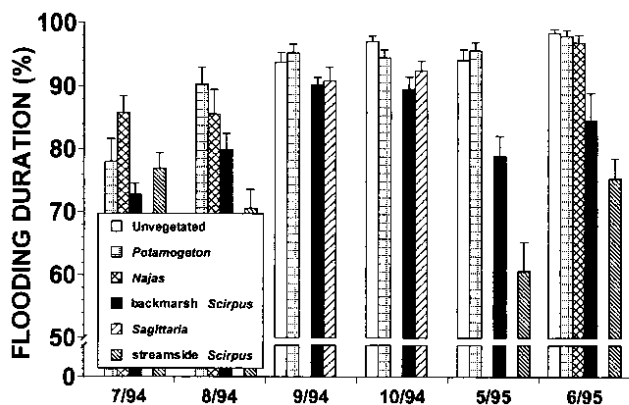


Fig. 5. Estimated mean monthly flooding duration [(hours habitat inundated)/(total hours in month) \times 100] for July through October 1994 and May and June 1995. Means and standard errors (SE) were calculated for 72 *Potamogeton* and backmarsh *Scirpus* sites, 48 streamside *Scirpus* and unvegetated sites, 36 *Najas* sites, and 24 *Sagittaria* sites. Bars are absent during months when that particular habitat type was not available for sampling. Error bars = 1 SE.

nificantly greater in flooded marsh than seagrass, or no significant difference was found between the two habitat types (except for brown shrimp *Farfantepenaeus aztecus* in May) (Rozas and Minello 1998). Although the tidal freshwater system we studied is floristically very different from the more saline system studied by Rozas and Minello (1998), our results are consistent with theirs in that densities of most species were similar in flooded marsh and SAV.

Dominant macrophyte species of marsh and SAV habitat types in our study area were morphologically very different. *Potamogeton* has relatively bare stems except for leaves located at their distal ends which form a thin, discontinuous layer of vegetation at the water surface. This layer of floating leaves appears complete enough to obscure the view of avian predators, although we observed little avian predation of nektonic organisms in our study area. *Najas* has numerous small, densely-packed, submerged leaves. *Scirpus* has slender, sometimes dense leaves that extend above the water surface. *Sagittaria* has emergent stems, similar in size to the *Scirpus* leaves, with ovate leaves at the ends.

Vegetation morphology has been shown to influence habitat use by fishes and crustaceans in previous work (Heck and Orth 1980a; Stoner and Lewis 1985; Bell and Westoby 1986a; Chick and McIvor 1994), but it did not seem to influence nekton distribution between SAV and marsh in our study. Protection from predators is likely provided by both SAV and marsh vegetation (West and Williams 1986; Wilson et al. 1987; Rozas and Odum 1988; Minello 1993), and any differences in refuge

value provided by SAV and emergent vegetation were apparently too little to influence habitat use.

Other factors that may affect nekton habitat use in SAV and flooded marsh are elevation and vegetation structural complexity. At high tide, killifish apparently prefer the high intertidal salt marsh, whereas penaeid shrimp remain in lower elevation, deeply flooded marsh (Kneib 1984; Rozas and Reed 1993). Although backmarsh *Scirpus* marsh and SAV substrate elevation differed by 6 to 12 cm during spring in our study, nekton densities generally differed little between these habitat types. Rozas and Minello (1998) also found that densities of most species did not differ between seagrass and flooded marsh in their study, where mean substrate elevations in marsh and seagrass differed by 11 cm. In contrast, Thomas et al. (1990) documented significantly higher densities of blue crabs in seagrass than *Spartina* marsh in most months sampled. The difference in blue crab densities between marsh and SAV found by Thomas et al. (1990) may be partially attributed to the relatively large difference in substrate elevation (24 cm) between the habitat types sampled (Rozas and Minello 1998).

The presence of SAV may have increased the structural complexity of emergent habitat types in our study area and thus may also have contributed to our finding few differences in nekton densities between flooded marsh and SAV. At some marsh sample sites, *Najas* or other species of SAV grew among *Scirpus* and *Sagittaria* stems. It is possible that this added structure attracted additional animals to emergent vegetation, including species more typically associated with SAV. Rozas and Minello (1998) also found aquatic vegetation (seagrass fragments) near *Spartina* stems at the marsh edge, and speculated about the possible habitat enhancement caused by this additional structure in marsh vegetation.

The presence of vegetation was apparently more important than the species or morphology of the existing vegetation in influencing nekton distribution among habitat types. Vegetated areas in the delta supported much higher densities of most nekton than unvegetated sites. Our results are consistent with numerous other studies conducted in estuaries that show an apparent selection of marsh or submerged vegetation over unvegetated bottom by fishes and crustaceans (Briggs and O'Connor 1971; Heck and Orth 1980b; Orth and Heck 1980; Zimmerman and Minello 1984; Rozas and Odum 1987a; Lubbers et al. 1990; Thomas et al. 1990; Williams et al. 1990; Sogard and Able 1991; Connolly 1994a,b; West and King 1996). Our study documents habitat usage only at high tide when all habitats are available for occupation by nekton. Undoubtedly, subtidal unvegetated bottom be-

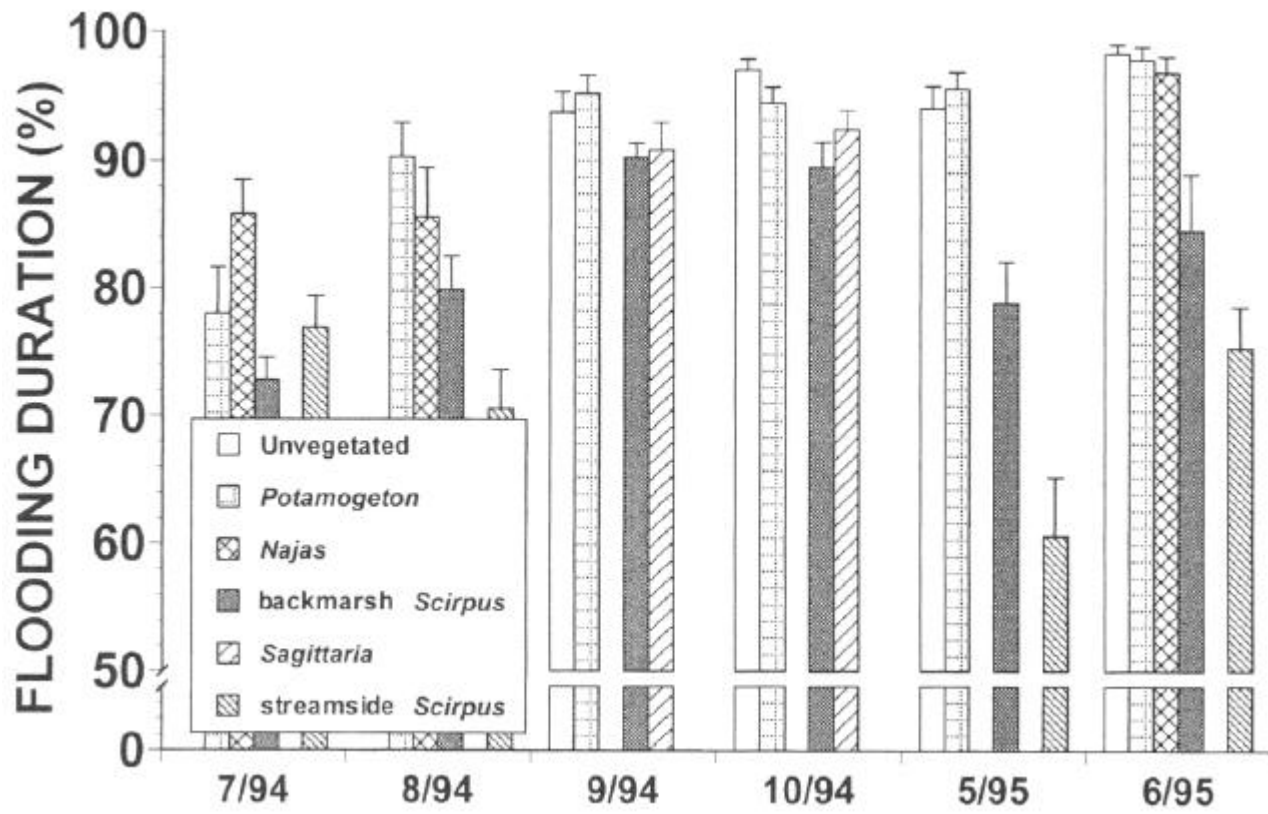


Figure 5.

comes more important for nekton during low-water events when marsh and intertidal SAV beds are exposed and therefore not usable. Although nekton and epifauna densities are often positively correlated with vegetation biomass (Adams 1976; Heck and Wetstone 1977; Heck and Orth 1980b; Stoner 1983; Heck and Thoman 1984; Lubbers et al. 1990; Montague and Ley 1993), we did not find a strong relationship despite high densities of nekton in vegetated habitat types (Castellanos 1997). The anomaly is most likely due to low animal densities associated with high vegetation biomass in streamside *Scirpus* marsh.

Higher nekton densities in vegetated than unvegetated areas are often ascribed to greater protection and more food provided by vegetated habitat types (Gilinsky 1984; Bell and Westoby 1986b; Rozas and Odum 1988; Fredette et al. 1990; Lubbers et al. 1990; Minello 1993). Palaemonid shrimp were preyed upon significantly less in vegetated than bare aquaria (Coen et al. 1981), and blue crabs in eelgrass *Zostera marina* suffered less predation compared to blue crabs on bare substrate (Heck and Thoman 1981; Wilson et al. 1987). In a tidal freshwater marsh, SAV provided predation protection for killifish (Rozas and Odum 1988). Vegetation supports greater standing crops of invertebrate prey organisms than unvegetated areas (Gerking 1962; Menzie 1980; Crowder and Cooper 1982; Lubbers et al. 1990; Connolly 1994b). Two studies indicate that some fishes eat more or larger prey in vegetated compared to unvegetated habitats (Rozas and Odum 1988; Lubbers et al. 1990). Although the foraging efficiency of fish predators may decrease when vegetation stem density or biomass becomes too great (Van Dolah 1978; Stoner 1982), this reduced foraging efficiency may be more than offset by the higher overall prey densities in vegetated than unvegetated areas (Rozas and Odum 1988). Prey densities may be insufficient on unvegetated substrate to support the high densities of nekton often found in vegetated habitat types.

Unlike most studies comparing SAV and unvegetated bottom in estuaries, in our study, presence of submerged vegetation was not confounded with water depth. Substrate elevations and flooding depths were not significantly different between SAV and unvegetated bottom. Therefore, differential water depth could not have played a role in the apparent selection of vegetated areas over unvegetated bottom that we found. Water depth may affect fish and crustacean distributions among estuarine habitats because predation rates may increase with water depth (McIvor and Odum 1988; Ruiz et al. 1993; Miltner et al. 1995).

Backmarsh areas may provide more valuable

habitat than streamside areas in the Atchafalaya Delta. The shallow elevational gradient across the backmarsh may provide a refuge for nekton that is lacking along stream channels (McIvor and Odum 1988). In addition to the refuge provided by shallow water, extensive SAV beds adjacent to backmarsh *Scirpus* may also afford protection as the tide drops, and organisms are forced out of the marsh (Rozas and Odum 1987b). Several species (sheepshead minnow, rainwater killifish, darter goby, and blue crab) were more abundant in at least one vegetated backmarsh habitat type than streamside *Scirpus* marsh. In contrast, only one species (freshwater goby) apparently selected streamside *Scirpus* over the backmarsh habitat types. Streamside *Scirpus* may be inferior as nursery habitat, particularly for blue crabs. In addition to the low numbers of blue crabs collected in streamside *Scirpus*, the mean sizes were generally larger and the habitat was devoid of the smallest juveniles (1–10 mm). In streamside marsh, water has only to recede a short distance from the vegetated marsh edge to force aquatic organisms into a deep channel usually devoid of SAV where they may be more susceptible to predation (McIvor and Odum 1988; Ruiz et al. 1993). Other factors that may be important are vegetation biomass and stem density. Vegetation biomass and stem density were higher in streamside *Scirpus* than backmarsh *Scirpus*. Streamside *Scirpus* may be a less desirable habitat if dense stems impede nekton movement in this habitat type. Although streamside and backmarsh habitat types consist of the same plant species, it is clear that in our study area and probably elsewhere, site specific characteristics are necessary to more accurately predict nekton usage.

Direct comparisons between our study and other investigations of similar habitats are difficult because few studies of nekton in low-salinity areas have employed quantitative sampling methods. However, in two such studies, researchers collected quantitative samples and reported nekton densities from vegetated habitat types. Rozas and Odum (1987a) used a 1-m² throw trap to sample submerged plant beds in tidal freshwater marsh channels in Virginia, and Zimmerman et al. (1990) sampled marsh and SAV at oligohaline sites in the Trinity River Delta, Texas using a 2.6-m² drop sampler. Palaemonid shrimps and blue crabs were the most abundant crustaceans collected in our study as well as these studies in Virginia and Texas. In samples from vegetated habitat types, blue crabs were generally less abundant (overall = 0.45 m⁻²) in Rozas and Odum (1987a) study and in the Zimmerman et al. (1990) study (0.1–3 m⁻²) than in our study. The high densities (up to 17 m⁻²) of blue crabs that we documented in fall were not

reported by Zimmerman et al. (1990). Daggerblade grass shrimp *Palaemonetes pugio* densities varied seasonally and ranged from 0–26 and 0–400 m^{-2} in the studies of Zimmerman et al. (1990) and Rozas and Odum (1987a), respectively. The only palaemonid shrimp collected in our study, riverine grass shrimp, was taken in densities ranging from 0–8 m^{-2} . In all three studies, most fishes taken in samples were from family Cyprinodontidae. Densities of total fishes were consistently higher in the Rozas and Odum (1987a) study (50–150 m^{-2} for most months) than total fish densities reported by Zimmerman et al. (1990) (0.69–13 m^{-2}) or our study (1.5–30.5 m^{-2}). The timing of sample collections may have contributed to the higher densities of grass shrimp and fishes reported from the Virginia study; submerged vegetation was sampled at low tide when animals were concentrated in subtidal marsh channels (Rozas and Odum 1987a).

Nekton assemblages of the shallow estuarine habitat types in our study area were dominated by small resident species of little direct economic value. However, blue crab, an important fishery species, was abundant in the study area in all seasons. Blue crabs were most numerous as small juveniles in vegetated areas in fall. Densities in our study area were high (up to 17 crabs m^{-2}) and comparable to values reported from more saline regions of Gulf Coast estuaries. Williams et al. (1990) reported blue crab densities as high as 14.4 m^{-2} in seagrass along the Alabama Gulf Coast. Zimmerman and Minello (1984) documented blue crab densities in a Texas salt marsh of 22.3 m^{-2} in November, but densities at other times of the year ranged from 2.6–15.0 m^{-2} . Thomas et al. (1990) found juvenile blue crab densities of up to 50.6 m^{-2} in a Texas seagrass bed, and up to 22.1 m^{-2} in *Spartina* marsh. Blue crabs were a more important component of the decapod crustacean assemblage in our study than in other studies of tidal freshwater systems where daggerblade grass shrimp greatly outnumbered other crustaceans (Rozas and Odum 1987a,b). The peak abundance of blue crabs we observed in fall reflects recruitment of small juveniles to shallow estuarine nursery areas (Herke and Rogers 1984; Williams et al. 1990). The Atchafalaya Delta may be an important nursery area for blue crabs on the Louisiana coast.

Although sciaenids are often abundant in Gulf Coast and Atlantic Coast estuaries (Weinstein 1979; Baltz et al. 1993), we collected only three individuals and species (Atlantic croaker *Micropogonias undulatus*, spot *Leiostomus xanthurus*, and one unidentified drum). Other studies conducted in tidal freshwater marsh have similarly reported few or no sciaenids (Rozas and Odum 1987a,b); however, Thompson and Deegan (1983) collected large

numbers of juvenile sciaenids by seining in the Atchafalaya Delta. Their samples were likely taken from channels where we also collected several juvenile sciaenids using a bait seine (Castellanos unpublished data). Young drum may seldom venture very far onto the shallow marsh; rather, they remain in deeper water near the marsh-channel interface (Baltz et al. 1993; Peterson and Turner 1994). Even though few commercially or recreationally important fish species occurred in the habitat types we sampled, the resident species found there in high abundance may provide food for larger, economically important predatory fishes (Darnell 1961; Hoese 1976).

The emerging Atchafalaya Delta contains important habitat for nekton. Submerged grass beds and flooded marsh appear to be equally important habitat for fishes and crustaceans in the Delta. Consistent with much of the literature, most nektonic species used vegetated areas in higher densities than unvegetated bottom. Also, most nekton appeared to prefer backmarsh habitat types over streamside marsh along channels. High densities of juvenile blue crabs in emergent vegetation and submerged grass beds are an indication of the important nursery function of vegetated habitat types in the Delta.

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